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Doctoral thesis

**Effects of enrichment on one-predator–two-prey
systems with different prey profitability**

(富栄養化が捕食者一種と栄養的価値の異なる被食者二種から成る系に
与える影響)

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要 旨

捕食者-被食者系において、富栄養化が進むと個体群動態が不安定化し、種の絶滅を招く可能性があることが理論的に報告されて以来、富栄養化が生態系に与える影響が注目されてきた。また富栄養化により、栄養的価値の低い「まずい」餌が優占することが知られている。そこで、1捕食者-2被食者系のモデルを用い、富栄養化が系を構成する個体群の平衡値と、系の安定性に与える影響を理論的に調べた。

捕食者が最適採餌をする場合、系の安定性（個体群振動の振幅の大きさ）は、まずい餌の栄養的価値の度合に強く依存し、特に、栄養的価値は低いを食べることができる時には系の安定性が大きく増すことが示された（第2章）。富栄養化すると、まずい餌の個体群が増加することは理論的にも経験的にも示されてきたが、おいしい餌の反応は理論的に統一されていなかった。ここでは、捕食者が湖沼などに棲むミジンコのようなおいしい餌もまずい餌も常にある比率で食べる捕食者の場合において、富栄養化とともにおいしい餌が増加するのはまずい餌の栄養的価値がある臨界値よりも低い時で、その臨界値より高ければ減少することが明らかにされた（第3章）。さらに、これまで未知とされてきたまずい餌の栄養的価値は、野外の湖沼のデータを編纂した文献を基に、この臨界値に近い値を取ると推量された。このミジンコ-藻類の系を、実験から得られた媒介変数値を用いて安定性を解析した（第4章）。3種が安定共存するかは、藻類2種の組合せに依存することが示された。3種安定共存が可能な場合、まずい餌の栄養的価値が上述の臨界値に近い時、富栄養化が進行しても共存平衡点が不安定化しにくいことも示され、自然界においてこの系が富栄養化に対して頑強であることを示唆している。

これらの結果は、まずい餌の存在が、捕食者の摂食様式にかかわらず、自然界の捕食者-被食者系の安定性に重要な役割を果たしていることを示唆する。

Chapter 1

General introduction

Enrichment, or often referred to as eutrophication, is an increasingly widespread and serious trend in natural ecosystems, and may become even more serious in the future due to an increased level of human activities. Special attention to effects of enrichment on ecosystems has been paid by ecologists since Rosenzweig (1971) implied decimation of species due to enrichment using several predator–prey models. This counterintuitive prediction is called the ‘paradox of enrichment’ after the title of his paper. It was subsequently modeled and confirmed by Gilpin (1972) and May (1972).

When we consider the problem of species extinction in theory, we should deal with the response of population abundance at equilibrium to enrichment as well as the stability of the system. This is because population which decreases its mean abundance and has large oscillation of abundance in the face of enrichment is much prone to extinction. In one-predator–two-prey systems, there is a regular trend that less profitable (therefore less vulnerable) prey increases in abundance with enrichment in theoretical (Phillips 1974; Vance 1978; Leibold 1989, 1996; Grover 1995) and in empirical works (Watson & McCauley 1988; Watson *et al.* 1992). On the other hand, there is not such a clear trend in the abundance of more profitable prey among theoretical works, although the empirical works (Watson & McCauley 1988; Watson *et al.* 1992) showed that the more profitable prey did not change in abundance with enrichment. These imply that the relative importance of the less profitable prey to the more profitable prey increases with enrichment.

Here I examine the effects of enrichment on one-predator-two-prey systems, especially in aquatic systems like zooplankton-phytoplankton interactions, because these aquatic systems are some of the theoretically and empirically best-studied systems. Algal prey are mechanically classified into two categories according to their cell sizes. Relatively small algae (often called nano-phytoplankton) are classified as the more profitable prey; larger algae (micro-phytoplankton) as the less profitable prey. As for the predator, I separately consider two type: an optimally selective predator like calanoid copepods and a generalist predator like *Daphnia*.

The thesis consists of four chapters including this. In Chapter 2, I deal with stability of a cyclic system, which is defined by the amplitude of population oscillation, in the case of an optimally selective feeding predator. Analysis for the population abundances at equilibrium in this case is omitted, because switching property produces discontinuous dynamics so that the accurate analysis for equilibrium is not possible. In the case of a generalist predator, I analyse the response of population abundances at equilibrium to enrichment in Chapter 3 and the stability at equilibrium in Chapter 4.

Chapter 2

Effects of enrichment on stability of a system with an optimally selective feeding predator

2.1 INTRODUCTION

A predator-prey model incorporating a natural assumption of satiation in predation has led to a paradoxical prediction (Rosenzweig 1971; Gilpin 1972; May 1972): a sufficient enrichment of the prey leads to the risk of destruction of the system. Such an enrichment first destabilizes a stable equilibrium point, resulting in a limit cycle. The amplitudes of the population oscillations will grow rapidly and, thus, the minimum population abundances will approach zero as enrichment is further increased, so that stochastic effects could lead to extinction (smaller populations are more prone to such an extinction). Thus, Rosenzweig (1971) warned against enriching natural ecosystems in order to increase their food yield.

In spite of the astonishing prediction of this classic model, the paradox has seldom been tested empirically. In one predator-one prey systems, there have been several experiments in which enrichment caused population oscillations (Huffaker *et al.* 1963; Luckinbill 1974; Bohannan & Lenski 1997). In contrast to these examples, McCauley & Murdoch (1990) showed by using a *Daphnia*-algal system that enrichment did not change the amplitude of the population oscillation, either in a field or an experimental system. Furthermore, Kirk (1998) showed with laboratory microcosms containing planktonic rotifer predators

and phytoplankton prey that enrichment can stabilize the population oscillations through autotoxins produced by the predator.

These empirical studies imply that it is necessary to apply additional assumptions to the theoretical model. For the empirical work by McCauley & Murdoch (1990), the presence of inedible prey is proposed as a plausible mechanism to resolve the discrepancy between theory and observation, in which the prey acts as a nutrient 'sponge' (Kretzschmar *et al.* 1993; Murdoch *et al.* 1998). The experiment by Kirk (1998) can be explained by the addition of density-dependent predator mortality to the classic model (Gilpin 1975), because this factor results in stabilizing an unstable system. Other models incorporating an assumption that the attack rate of the predator depends on the ratio of prey to predator abundances claim that enrichment is not predicted to be destabilizing (Arditi & Ginzburg 1989). These 'ratio-dependent' models, however, are less widely accepted than 'prey-dependent' models in which the attack rate depends on the instantaneous density of prey (Oksanen *et al.* 1992; Diehl *et al.* 1993; Abrams 1994; Gleeson 1994).

In this chapter, I theoretically propose a new mechanism that resolves the paradox of enrichment, using a one predator–two prey model in which the predator shows optimal selective feeding, which is a well known behaviour of many predators (Werner & Hall 1974; Krebs *et al.* 1977; DeMott 1989). Several studies have shown that switching between prey by predators can stabilize predator–prey systems (Murdoch 1969; Murdoch & Oaten 1975; Tansky 1978; Teramoto *et al.* 1979). However, none of these studies considered cases in which the equilibrium was unstable and the system followed a limit cycle. The model applied here is different from the previous models with switching predators in (i) that

I deal with non-equilibrium dynamics of limit cycles and (ii) that the predator displays the optimal selective feeding strategy which maximizes energy input, dependent on the profitabilities and the abundances of its prey (Charnov 1976). I assume that enrichment of a system increases only the prey carrying capacity, following the original model in which the paradox of enrichment was discussed (Rosenzweig 1971). It is well known that the stability of an equilibrium point depends on the carrying capacity, but not on the intrinsic growth rate which may affect the equilibrium abundance.

2.2 MODEL

Consider a system consisting of two prey species populations (X_1 and X_2) and one predator population (Y), whose dynamics is defined by the following set of equations:

$$\frac{dX_1}{dt} = \left\{ \varepsilon_1 \left(1 - \frac{X_1}{K_1} - \alpha \frac{X_2}{K_1} \right) - r_1 Y \right\} X_1 \quad (2.1a)$$

$$\frac{dX_2}{dt} = \left\{ \varepsilon_2 \left(1 - \beta \frac{X_1}{K_2} - \frac{X_2}{K_2} \right) - r_2 Y \right\} X_2 \quad (2.1b)$$

$$\frac{dY}{dt} = \{-\varepsilon_3 + k(g_1 r_1 X_1 + g_2 r_2 X_2)\} Y \quad (2.1c)$$

where $r_i = p_i a_i / (1 + \sum_j p_j h_j a_j X_j)$.

The parameters ε 's and K 's are the rates of growth of the two prey when scarce (ε_3 is the predator death rate) and the carrying capacities of the prey in the environment, respectively. The two prey species compete with each other, described by a Lotka-Volterra competitive system with interspecific competition coefficients α and β . The energy value

of an individual of prey species i is g_i . The conversion efficiency of consumed prey into the predator's reproduction rate is k . The term r_i corresponds to predation, in which the encounter efficiency with prey species i is a_i ; the handling time for prey species i is h_i ; p_i is the probability that the predator captures an individual of prey species i when encountered. I assume here that the predation is basically described by a type 2 functional response (concave downwards), because I am interested in the dynamics of an unstable system and the type 2 is the simplest functional response that produces a population oscillation.

Assume that the predator is an optimal forager that chooses the value for each of the probabilities p_i ($0 \leq p_i \leq 1; i = 1, 2$) so as to maximize the energy input by predation $g_1 r_1 X_1 + g_2 r_2 X_2$. The two prey species are assumed to be ranked in their profitability as $g_1/h_1 > g_2/h_2$ (i.e. prey X_1 is more profitable for the predator than prey X_2) so that p_1 should always be 1 (Charnov 1976). I also assume that the more profitable prey X_1 is superior in competition to the less profitable prey because, otherwise, the two prey species cannot coexist (Takeuchi 1996). I further assume that the more profitable prey X_1 yields nutrition enough to support a persisting predator population in the absence of the less profitable prey, or mathematically, that

$$g_1/h_1 > \varepsilon_3/k. \quad (2.2)$$

This inequality is derived from the condition that there exists a positive range of X_1 such that $dY/dt > 0$ when $X_2 = 0$ and $Y > 0$ in equation (2.1c).

It is known (Charnov 1976) that the predation rate $g_1 r_1 X_1 + g_2 r_2 X_2$ is maximized

when $p_2 = 0$ (or $p_2 = 1$) if the abundance of the more profitable prey X_1 is greater (or smaller) than a critical abundance \hat{X}_1 , where $\hat{X}_1 = g_2/[a_1 h_1 h_2 (g_1/h_1 - g_2/h_2)]$.

Noting that \hat{X}_1 is an increasing function of the profitability g_2/h_2 of the less profitable prey X_2 , let the prey be classified, according to the range of its profitability g_2/h_2 , that is, the value of \hat{X}_1 , into three categories: inedible prey ($\hat{X}_1 < X_1^{min}$), unpalatable prey ($X_1^{min} < \hat{X}_1 < X_1^*$), and palatable prey ($X_1^* < \hat{X}_1$), where X_1^{min} is the minimum abundance of X_1 in its oscillation when $X_2 = 0$, and $X_1^* (\equiv \varepsilon_3/[a_1(kg_1 - \varepsilon_3 h_1)])$ is the equilibrium value of X_1 when $X_2 = 0$, obtained from $dY/dt = 0$ in equation (2.1c) with $Y > 0$. Note that X_1^{min} and X_1^* do not depend on g_2 or h_2 .

Setting $\hat{X}_1 = X_1^*$, I obtain the critical profitability of X_2 , ε_3/k , below which (i.e. $g_2/h_2 < \varepsilon_3/k$) the less profitable prey is classified as unpalatable and above which ($g_2/h_2 > \varepsilon_3/k$) it is classified as palatable. Note from inequality (2.2) that an unpalatable or inedible prey cannot, while a palatable prey can, yield nutrition enough to support the predator population in the absence of the alternative prey.

2.3 RESULTS

I numerically calculated the dynamics of three species for different profitability of the less profitable prey and summarized the results in figure 2.1. We first observe that in the absence of the less profitable prey X_2 , population oscillations occur with sufficient enrichment, that is, for large values of K (the left-most panels in figure 2.1a, b). The presence of X_2 always reduces the amplitude of oscillation (the other panels in figure

2.1a, b). The degree of this stabilizing effect depends on the profitability g_2/h_2 of the less profitable prey X_2 (figure 2.1a, b, d). The stabilizing effect is the strongest when the less profitable prey is unpalatable. Within the range of unpalatable prey, the stabilizing effect becomes stronger as the profitability g_2/h_2 of the less profitable prey X_2 increases and the oscillation is sharply suppressed (almost to a negligible level) at the critical profitability of the prey, ϵ_3/k , beyond which the amplitude of the oscillation discontinuously increases (figure 2.1d).

In the presence of inedible prey X_2 , the effective carrying capacity of X_1 is reduced by competition (Kretzschmar *et al.* 1993), resulting in reduction in the amplitude of the oscillation. In the presence of unpalatable prey X_2 , observe a vertical drop of the orbit in the X_1 - Y space (figure 2.1b). A close-up view of the drop (figure 2.1c) indicates the following: an expanded population Y causes the reduction of X_1 , but, once X_1 falls below \hat{X}_1 , the predator begins to eat not only X_1 but also X_2 , which causes an immediate recovery of X_1 , while decreasing Y itself (because $\hat{X}_1 < X_1^*$, where $dY/dt < 0$, as is clear from equation (2.1c)). As the profitability g_2/h_2 of the unpalatable prey X_2 increases, the \hat{X}_1 value and, thus, the realized minimum X_1 value increase, which causes the minimum Y to increase, resulting in the reduction in the amplitude of the oscillation (figure 2.1d).

In the case of palatable prey X_2 , its population level is more heavily suppressed both by predation due to its relatively high profitability and by competition with the superior competitor X_1 . The competitive influence of X_2 on X_1 is thus reduced, resulting in a larger value of the maximum X_1 as shown in figure 2.1a. The maximum Y is enhanced not only by the large value of the maximum X_1 but also by a relatively high profitability of X_2 , which subsequently causes the small values of the minimum X_1 and Y . Thus, the

amplitude of the oscillation in the case of palatable prey is larger than that in the case of inedible prey (figure 2.1*d*).

Next, I examine the effects of increasing enrichment, or the carrying capacity K , on the oscillation amplitude and the minimum abundance of prey X_1 under the presence of different categories of prey X_2 . In the case of unpalatable prey, the minimum abundances of all the species populations are kept considerably higher than zero in the face of increasing enrichment, while they approach to zero in the other cases (figure 2.2*a*). This means that an unpalatable prey prevents the abundances of all the species populations from becoming so low that stochastic fluctuation may cause them to go extinct. Although the amplitude of the population oscillation increases with an increasing enrichment in the case of any category of the less profitable prey, the increase is much slower in the case of unpalatable prey (figure 2.2*b*). Thus, unpalatable prey most effectively prevents the system from oscillating to population extinction in the face of increasing enrichment, resolving the puzzle over the paradox of enrichment.

2.4 DISCUSSION

As to the effect of enrichment on the parameters, I followed a historical manner that enrichment of the prey caused only a change in the carrying capacity, but one might imagine that enrichment can cause an increase in the intrinsic growth rate (ϵ_1 and ϵ_2), or further both in the intrinsic growth rate and the carrying capacity. I preliminarily confirmed by numerical simulation that an increase in the intrinsic growth rate had little

effect on the amplitude of the population oscillation, in contrast to an increase in the carrying capacity, and caused the cycle to move upward in the X_1 - Y space (which corresponded to an increase in the predator equilibrium abundance). Therefore, if enrichment increased only the intrinsic growth rate, there would not exist the problem of the ‘paradox of enrichment’ in the first place. This is the reason why I confined my study to effects of the carrying capacity on dynamics of the system.

My model with an optimally foraging predator which maximized its energy intake, revealed that the stabilizing effect of the alternative (less profitable) prey species was strongest when it yielded insufficient nutrient on its own to maintain the predator population but its profitability was relatively high (i.e. unpalatable prey). The relationship between the profitability of the less profitable prey and the amplitude of the population oscillation in figure 2.1*d* showed a discontinuous change between the categories, unpalatable and palatable prey, which is a new result in the stability analyses of communities. This discontinuous change implies the possibility that a population oscillation with small amplitude can explosively increase due to a small change in the profitability of the less profitable prey, for example, in the handling time in response to a change in temperature or in the energy value of individual prey in response to enrichment of the system. The reversed scenario that the amplitude is suddenly reduced is also possible. These could occur when the profitability of the less profitable prey takes a value near the critical profitability ε_3/k .

My assumption of optimal behaviour by the predator was shown to prevent the paradoxical prediction as to enrichment: in the presence of unpalatable prey, though the amplitude of the population oscillation increased somewhat with enrichment, the mini-

mum abundance of the more profitable prey species was kept well above zero and, thus, the minimum abundance of the predator was subsequently kept considerably higher than zero, so that the predator-prey system was robust against any magnitude of enrichment. There have been theoretical works with other assumptions of adaptive behaviour by predators and prey which can stabilize population oscillations, although most of these works dealt with only the stability of the equilibrium points. Selective feeding by predators, in which they fed more intensively on the more abundant prey species, was shown to broaden the condition under which the equilibrium point was stable (Murdoch 1969; Murdoch & Oaten 1975; Tansky 1978; Teramoto *et al.* 1979). Antipredator behaviours of prey can also stabilize population oscillations in a system with heterogeneity such as refuges in which the predation risk is low but the prey has some disadvantage (Ruxton 1995; Krivan 1998). In conclusion, adaptive behaviours of predator and prey have a general tendency to make it harder for predators to overexploit a specific prey and so can have stabilizing effects.

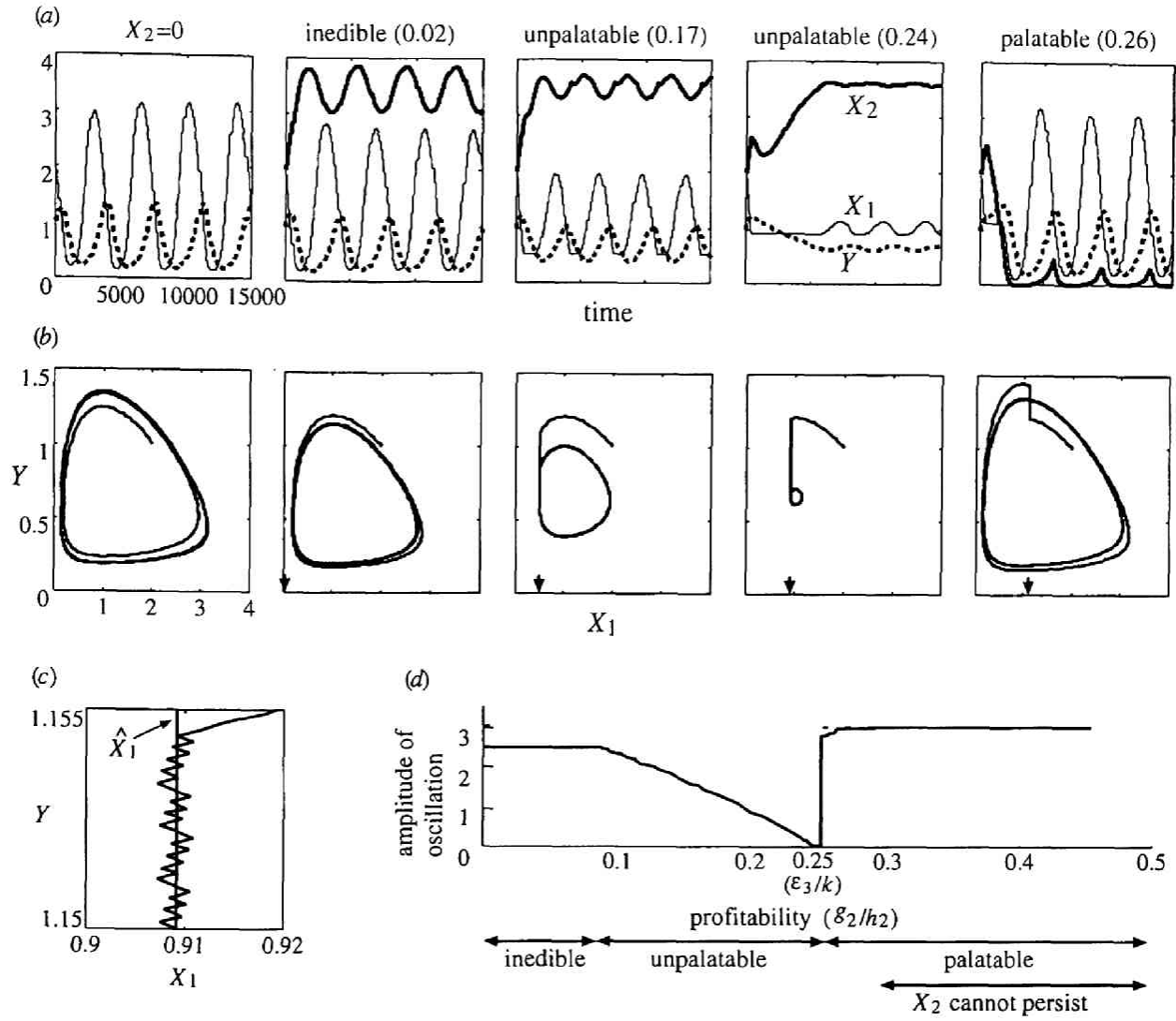


Figure 2.1 Dynamics of the predator-prey system described by equations (2.1) with the less profitable prey of different degrees of profitability. I solved numerically by the Runge-Kutta method using the following values: $\varepsilon_1 = 0.5, \varepsilon_2 = 0.25, \varepsilon_3 = 0.25, \alpha = 0.1, \beta = 0.4, a_1 = a_2 = 1, k = 1, g_1 = g_2 = 0.5, h_1 = 1, K_1 = K_2 = 4$. I change the profitability g_2/h_2 of the less profitable prey X_2 by changing the h_2 value. (a) The temporal change in abundances of the more profitable prey (X_1 , thin line), less profitable prey (X_2 , thick line) and predator (Y , dotted line), and (b) the dynamics in the X_1 - Y space of the system. Panels in (a) and (b) in the same column depict the same case. Numbers in parentheses in (a) express the profitability of the less profitable prey. Arrows in (b) express the values of \hat{X}_1 . In the left-most panels of (a) and (b): the less profitable prey X_2 is absent; the initial values are $(X_1, X_2, Y) = (2, 0, 1)$; the equilibrium point in the X_1 - Y space is $(1, 0.75)$. In the other panels: the initial values are $(2, 2, 1)$; the equilibrium point is $(1, 0.66)$. (c) A close-up view of the vertical drop in the X_1 - Y space in the case of the unpalatable prey X_2 with profitability $g_2/h_2 = 0.24$. (d) Relationship between the profitability g_2/h_2 of the less profitable prey X_2 and the amplitude of the oscillation, defined by the difference between the maximum and minimum abundances of the more profitable prey X_1 . The broken line represents the amplitude of the oscillation in the absence of the less profitable prey X_2 . The profitability g_1/h_1 of the more profitable prey X_1 is 0.5.

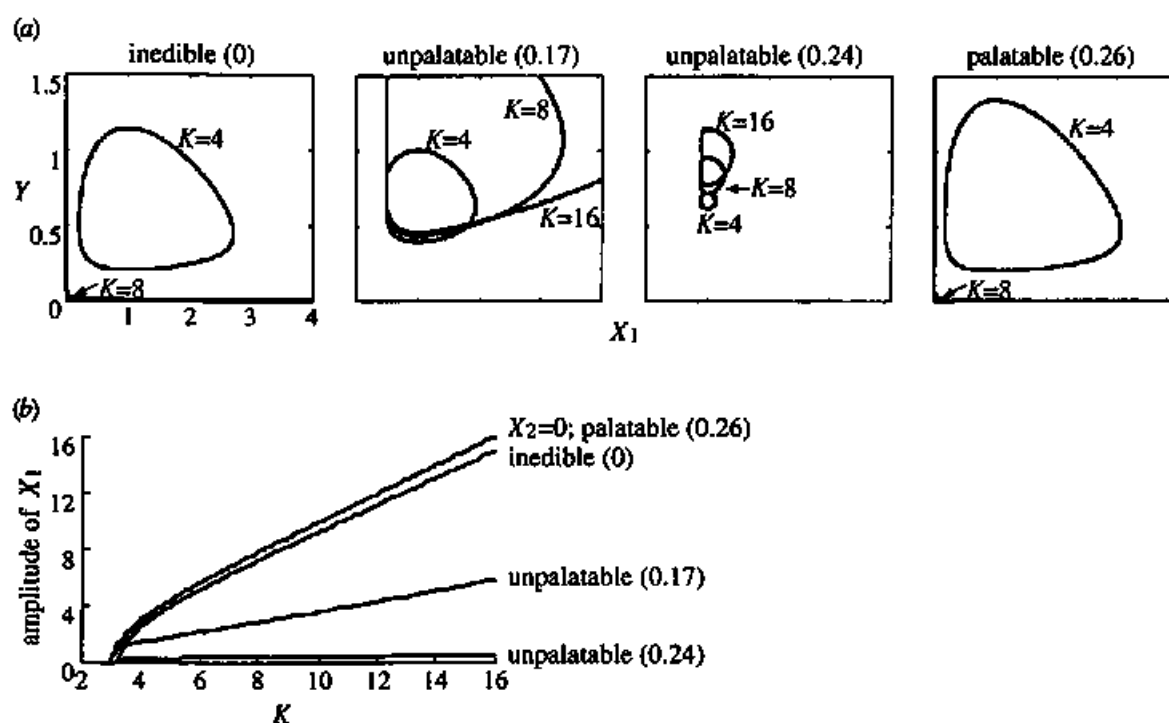


Figure 2.2 Effects of enrichment in the presence of the less profitable prey with different profitability values. Numbers in parentheses express the profitability g_2/h_2 of the less profitable prey X_2 . The degree of enrichment is represented by the magnitude of the prey carrying capacity, K ($= K_1 = K_2$). The other parameters are the same as in figure 2.1. (a) Minimum abundances on the limit cycles in the X_1 - Y space. In the case of inedible and palatable prey, the orbits with $K = 16$ almost cling to the axes. (b) Relationship between enrichment and the amplitude of the oscillation, defined as the same as in figure 2.1d.

Chapter 3

Effects of enrichment on the response of population abundances in a system with a generalist predator

3.1 INTRODUCTION

The abundance of the less profitable prey in a one-predator–two-prey system has shown to increase with enrichment theoretically (Phillips 1974; Vance 1978; Leibold 1989, 1996; Grover 1995) and empirically (Watson & McCauley 1988; Watson *et al.* 1992), whereas the response of the more profitable prey abundance has not been clear. This problem on the response (i.e. the more profitable prey *increases* or *decreases* with enrichment) is critical, because the prey is the main resource supporting the system.

Many theoretical models predict that the more profitable prey decreases with enrichment (Phillips 1974; Vance 1978; Leibold 1989, 1996), while another model predicts that it increases (Grover 1995). Although these models have assumed the less profitable prey as inedible, it is not always clear how profitable the less profitable prey is actually for the predator (Leibold 1989; Murdoch *et al.* 1998). In this chapter, changing this unknown profitability of the less profitable prey, I investigate the response of population abundances to enrichment in a one-predator–two-prey system.

Here I focus on a system consisting of a predator species, like a generalist filter feeder *Daphnia*, and two prey species, like two species of algae, with different profitability. The *Daphnia*–algal system is one of the most widespread and best studied systems in lakes. For

Daphnia, unicellular algae (often called nano-phytoplankton) are more profitable, while larger algae (micro-phytoplankton) are less profitable (Sterner 1989; Kretzschmar *et al.* 1993). The ratio of the surface area to the volume of algal cells decreases with the cell size, so smaller algae are generally superior in nutrient competition. The functional response of *Daphnia* can be well described by a type 2 equation (DeMott 1982; Paloheimo *et al.* 1982; Porter *et al.* 1982). There exists a difference in vulnerability between the two prey and the less profitable prey cannot be perfectly excluded from *Daphnia*'s diet, because *Daphnia* mechanically selects its prey by filtering comb. Using a theoretical model that incorporates these features, I investigate the response of the equilibrium abundances to enrichment defined as an increase in the total amount of nutrient in the system.

3.2 MODEL

I use the following set of differential equations:

$$dX_1/dt = \mu_1(N)X_1 - \epsilon_1 X_1 - r_1(X_1, X_2)Y \quad (3.1a)$$

$$dX_2/dt = \mu_2(N)X_2 - \epsilon_2 X_2 - r_2(X_1, X_2)Y \quad (3.1b)$$

$$dY/dt = -\epsilon_3 Y + k(g_1 r_1(X_1, X_2) + g_2 r_2(X_1, X_2))Y \quad (3.1c)$$

and

$$N + g_1 X_1 + g_2 X_2 + g_3 Y = T, \quad (3.1d)$$

where X_1 , X_2 and Y are the abundances of the more profitable prey, the less profitable prey and the predator, respectively. Parameters are: $\mu_i(N)$, the nutrient-dependent reproductive rate of prey i ($i = 1, 2$); ε_i (or ε_3), the density-independent loss rate of prey i (or predator); $r_i(X_1, X_2)$, the functional response of the predator modified to include two prey species; g_i (or g_3), the amount of nutrient bound in an individual of prey i (or predator); k , the conversion efficiency of the nutrient into the predator's reproduction rate; T , the total amount of nutrient in the system. The equation for the nutrient dynamics (N) is not necessary in this closed system because of a simple algebraic mass balance expression in equation (3.1d). I define as the degree of enrichment the total amount of nutrient, T , in the system, as is commonly used in empirical studies (e.g. total phosphorus in lakes), rather than the carrying capacity or the intrinsic growth rate of prey which is biologically obscure with relation to enrichment (Abrams & Roth 1994).

According to Kretzschmar *et al.* (1993) and Grover (1995), the two-prey-species version of the functional response of *Daphnia* is expressed by

$$r_i(X_1, X_2) = \frac{a_i X_i}{1 + h_1 a_1 X_1 + h_2 a_2 X_2},$$

where a_i and h_i are, respectively, the consumption efficiency of and the handling time for, prey i . Since prey 1 is more profitable for, and more vulnerable to, the predator than prey 2, the following inequalities hold:

$$g_1/h_1 > g_2/h_2 \quad \text{and} \quad a_1 > a_2. \quad (3.2)$$

I assume that the more profitable prey X_1 is superior in nutrient competition to the less profitable prey X_2 , because otherwise the two prey cannot coexist (Takeuchi 1996). I also assume that the more profitable prey yields enough nutrition to support a persisting predator population in the absence of the less profitable prey as in Chapter 2 (equation (2.2)), which mathematically requires

$$g_1/h_1 > \varepsilon_3/k. \quad (3.3)$$

3.3 RESULTS

In the X_1 - X_2 space (figure 3.1), the equilibrium abundances of the two prey are given as the intersection point of the two lines represented by the following equations:

$$(kg_1 - h_1\varepsilon_3)a_1X_1 + (kg_2 - h_2\varepsilon_3)a_2X_2 = \varepsilon_3 \quad (3.4a)$$

$$(g_1 + g_3h_1a_1c)X_1 + (g_2 + g_3h_2a_2c)X_2 = T - N^* - g_3c, \quad (3.4b)$$

where $c = (\mu_1(N^*) - \varepsilon_1)/a_1 = (\mu_2(N^*) - \varepsilon_2)/a_2$ and ‘*’ denotes a value at equilibrium. Equation (3.4a) is derived from equation (3.1c) (the right hand side equaling zero) and equation (3.4b) from equations (3.1a) and (3.1d). Line (3.4a), which is given by equation (3.4a), has a negative slope if $g_2/h_2 > \varepsilon_3/k$ (figure 3.1a), and a positive slope if $g_2/h_2 < \varepsilon_3/k$ (figure 3.1b). Line (3.4b), which has been referred to as a mass-balance constraint (Holt *et al.* 1994), has always a negative slope, and moves away from the origin as T increases. The slope of line (3.4a), when negative, is always steeper than that of line

(3.4b) under the condition given in inequalities (3.2) (Appendix 3.A). Thus, the response of the prey abundances at equilibrium to enrichment (indicated as an increase in T from a lower level T_1 to a higher level T_2) exhibits two qualitatively different patterns depending on the profitability of the less profitable prey, g_2/h_2 . The equilibrium abundance of the more profitable prey (X_1^* , the X_1 -coordinate of the equilibrium point, indicated as the intersecting point of the two lines in figure 3.1) decreases while that of the less profitable prey (X_2^*) increases if the profitability of the less profitable prey (g_2/h_2) is higher than a critical value ε_3/k so that the slope of line (3.4a) is negative (figure 3.1a), whereas both increase otherwise (figure 3.1b). Because, as seen from inequality (3.3), a less profitable prey with a profitability $g_2/h_2 > \varepsilon_3/k$ can yield sufficient nutrition to support the predator population in the absence of the more profitable prey, while a prey with a profitability $g_2/h_2 < \varepsilon_3/k$ cannot even at high densities, let the less profitable prey be called a ‘palatable’ prey for the former case and an ‘unpalatable’ prey for the latter case.

The equilibrium concentration of the nutrient (N^*), which is obtained from equations (3.1a) and (3.1b), is independent of the degree of enrichment (T) as long as the two prey coexist (figure 3.2). The equilibrium abundance of the predator (Y^*) always increases with enrichment (Appendix 3.A). When the less profitable prey (X_2) is palatable, the decline of the more profitable prey with enrichment finally leads to its extinction, resulting in a one-predator–one-prey system, as shown in figure 3.2a. In this reduced system, both the nutrient concentration and the predator abundance increase, whereas the less profitable prey abundance remains unchanged, with a further enrichment, as shown by previous works (Grover 1995; Leibold 1996). As the profitability of the less profitable prey (g_2/h_2) decreases (the transition: $a \rightarrow b \rightarrow c \rightarrow d$ in figure 3.2), the rate of increase in the

equilibrium abundance of the more profitable prey (the slope of the line representing X_1^* in figure 3.2) increases so that it turns from negative (figure 3.2*a, b*; corresponding to figure 3.1*a*) into positive (figure 3.2*c, d*; corresponding to figure 3.1*b*). When the less profitable prey has a profitability close to the critical value ε_3/k , X_1^* scarcely changes with enrichment (figure 3.2*b, c*).

3.4 DISCUSSION

The equilibrium abundance of the less profitable prey increased with enrichment, independent of its profitability, as shown in the previous models (Phillips 1974; Vance 1978; Leibold 1989, 1996; Grover 1995). The outcome of my model with respect to the predator abundance conforms to some of these models in which the predator increases in abundance with enrichment (Leibold 1989; Grover 1995), but differs from other models in which the predator does not change in abundance (Phillips 1974; Leibold 1996). As for the more profitable prey, the response was dependent upon the profitability of the less profitable prey. The two qualitatively different predictions made by previous models can be interpreted in the context of my model, although some of these models define enrichment in slightly different ways. In one prediction where the more profitable prey decreases in abundance with enrichment (Phillips 1974; Vance 1978; Leibold 1989, 1996), a linear functional response was assumed (the case $h_4 = 0$ in my model, and hence the profitability is infinity), implying that the less profitable prey was able to support the predator population by itself unless it is completely valueless (i.e. $g_2 \neq 0$), which corresponds to a

'palatable' prey in my model. On the other hand, in the other prediction where the more profitable prey increases in abundance with enrichment (Grover 1995), the less profitable prey was assumed not to yield any nutrition to the predator ($g_2 = 0$), corresponding to an 'unpalatable' prey in my model. These qualitatively different responses of the more profitable prey abundance may be explained by the reason that although enrichment leads in general to increases in both prey abundances, the presence of a less profitable but palatable prey suppresses strongly the more profitable prey by raising the abundance of the common predator, namely, the effect of apparent competition (Holt 1977).

Leibold (1989) summarized results from numerous experiments involving nutrient enrichment, in which the most general outcome was an increase in all abundances of more profitable (edible) prey, less profitable (inedible) prey, and predators (herbivores). According to my model, this outcome suggests that the less profitable prey was nutritionally inadequate to support the predator populations in the absence of the more profitable prey. In this sense, the prey could be called unpalatable prey. Moreover, other compiled empirical data (Watson & McCauley 1988; Watson *et al.* 1992) showed that the less profitable prey increased largely whereas the more profitable prey scarcely changed, with increasing total phosphorus, suggesting that the profitability of the less profitable prey in these cases was close to the critical value ε_3/k .

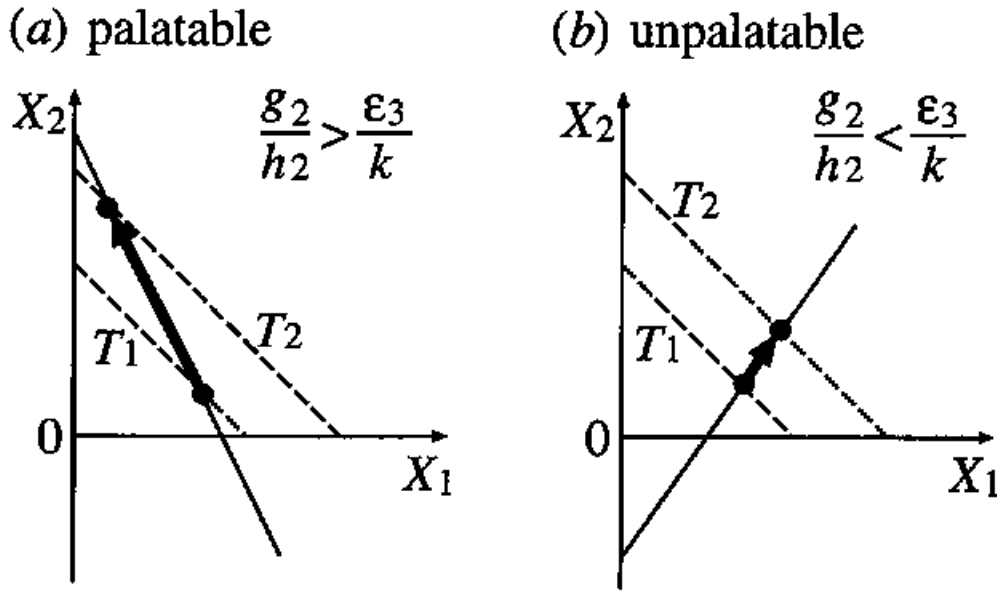


Figure 3.1 Graphical representation of the effects of enrichment on the abundances of two competing prey, the more profitable prey (X_1) and the less profitable prey (X_2), in the X_1 - X_2 space (a) when the less profitable prey is palatable, i.e. $g_2/h_2 > \epsilon_3/k$ and (b) when the prey is unpalatable, i.e. $g_2/h_2 < \epsilon_3/k$. Their equilibrium abundances are expressed by an intersection point of solid line (corresponding to equation (3.4a)) and dashed line (corresponding to equation (3.4b)). The dashed line moves away from the origin as the system is enriched, which is defined as an increase in the total amount of nutrient (T) in the system ($T_1 < T_2$).

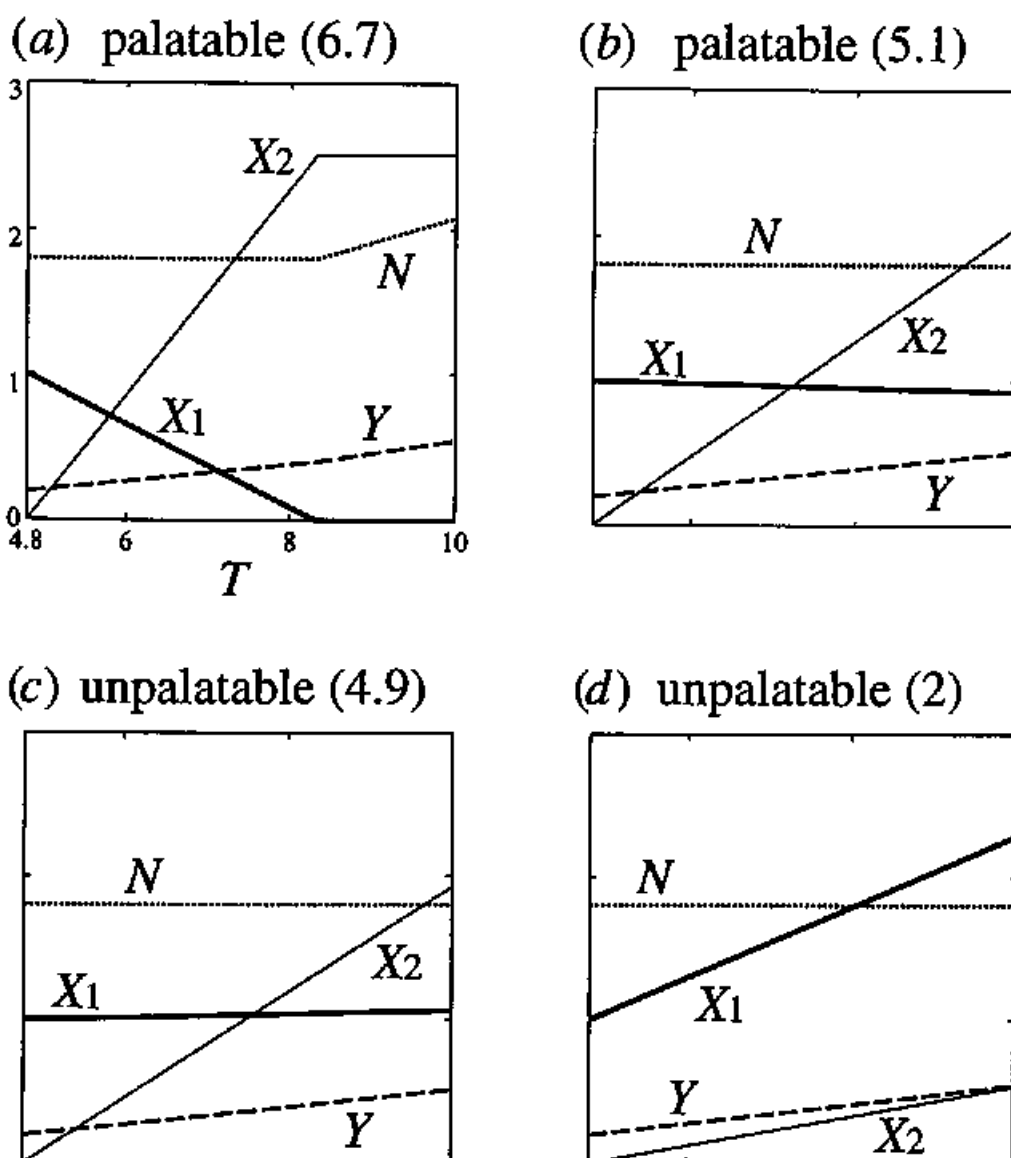


Figure 3.2 Examples of the response of the nutrient (dotted line), the more profitable prey (thick line), the less profitable (thin line) and the predator (dashed line) at equilibrium to enrichment (a, b) when the less profitable prey is palatable, i.e. $g_2/h_2 > \varepsilon_3/k$ and (c, d) when the prey is unpalatable, i.e. $g_2/h_2 < \varepsilon_3/k$. The degree of enrichment is defined as the total amount of nutrient (T) in the system. I assumed that $\mu_i(N) = b_i N$ ($i = 1, 2$). The following parameter values were used: $b_1 = b_2 = 1$, $\varepsilon_1 = 0.8$, $\varepsilon_2 = 1$, $a_1 = 10$, $a_2 = 8$, $g_1 = g_2 = 1$, $h_1 = 0.1$, $\varepsilon_3 = 0.5$, $k = 0.1$, $g_3 = 10$. I changed the profitability of the less profitable prey (g_2/h_2 , numbers in parentheses) by changing h_2 . The critical profitability (ε_3/k) is 5 and the profitability of the more profitable prey (g_1/h_1) is 10.

APPENDIX 3.A

The equilibrium abundance of the predator and the steepness of lines given by equations (3.4)

The equilibrium abundance of the predator (Y^*) is given from equations (3.1b-d) by

$$Y^* = \frac{kh_1h_2a_1a_2c(g_1/h_1 - g_2/h_2)}{a_1(kg_1 - h_1\epsilon_3)(g_2 + g_3h_2a_2c) - a_2(kg_2 - h_2\epsilon_3)(g_1 + g_3h_1a_1c)}T + \text{constant}, \quad (3.A1)$$

where $c = (\mu_1(N^*) - \epsilon_1)/a_1 = (\mu_2(N^*) - \epsilon_2)/a_2$ and the 'constant' term is independent of T . The numerator is positive under the condition given in inequalities (3.2) (hereafter I call condition (3.2)). The denominator is also positive if

$$\{(p_1 + sa_1)a_2 - (p_1 - q)a_1\}p_2 < (q + sa_1)p_1a_2,$$

where $p_i = g_i/h_i$, $q = \epsilon_3/k$, $s = g_3c$. This is equivalent to

$$p_2 < f(a_2) \quad \text{when} \quad a_2 > \hat{a}_2 \quad (3.A2a)$$

$$p_2 > f(a_2) \quad \text{when} \quad a_2 < \hat{a}_2, \quad (3.A2b)$$

where $f(a_2) = (q + sa_1)p_1a_2/\{(p_1 + sa_1)a_2 - (p_1 - q)a_1\}$ and $0 < \hat{a}_2 = (p_1 - q)a_1/(p_1 + sa_1) < a_1$. It is obvious that condition (3.A2b) always holds because $f(a_2) < 0$. Since $f(a_2)$ is a decreasing function of a_2 , it takes its minimum p_1 at $a_2 = a_1$ in the interval, $\hat{a}_2 \leq a_2 \leq a_1$. Thus, condition (3.A2a) is also satisfied as long as $p_2 < p_1$ and $a_2 < a_1$. Therefore,

$dY^*/dT > 0$ under condition (3.2).

'The slope of line (3.4*a*), when negative, is steeper than that of line (3.4*b*)' is mathematically equivalent to 'the denominator of the coefficient of T in equation (3.A1) is positive' which has already been proved above under condition (3.2).

Chapter 4

Effects of enrichment on stability of a system with a generalist predator

4.1 INTRODUCTION

Enrichment in a predator-prey system leads in theory to destruction of a stable equilibrium (Rosenzweig 1971; Gilpin 1972; May 1972). Further, a limit cycle caused by destabilization of the equilibrium point has a potential to result in stochastic extinction of species. On the other hand, instability with enrichment does not always occur in experimental and natural communities (McCauley & Murdoch 1990), puzzling us as to the effect of enrichment on stability of ecosystems.

In a system consisting of an optimally selective feeding predator, like many copepods, and two prey with different profitability, the stability defined by the amplitude of the population oscillation depends on the profitability of the less profitable prey (Chapter 2). Specifically, the presence of a less profitable but edible (thus unpalatable) prey increased the stability of the system. In Chapter 3, I analysed the response of population abundances at equilibrium to enrichment in a system consisting of a generalist predator like a filter feeder *Daphnia* and two prey species with different profitability, where the analysis for stability was omitted. Here I focus on the stability of the system, especially on the relationship between the stability and the profitability of the less profitable prey along a gradient of enrichment.

The prey considered here differ in profitability for the predator. One prey is labeled the more profitable prey, corresponding to relatively small algae (nano-phytoplankton). The other is labeled the less profitable prey, corresponding to larger algae (micro-phytoplankton). Although the latter prey has been viewed as inedible by previous works (e.g. Leibold 1989; Kretzschmar *et al.* 1993; Grover 1995; Murdoch *et al.* 1998), I regard the prey as one that can yield some nutrition to the predator because the nutritional values of the so-called inedible algae are various (Leibold 1989; Murdoch *et al.* 1998). Consumption of algae by a generalist filter feeder *Daphnia*, considered here as the predator, is often well described by a type 2 functional response (DeMott 1982; Paloheimo *et al.* 1982; Porter *et al.* 1982). This functional response is a factor generating instability in predator-prey systems when the system is enriched (May 1972). My model includes the dynamics of nutrient, because many of empirical works use the total amount of nutrient (e.g. total phosphorus in lakes) as an indicator of enrichment.

As is often the case with stability analyses of systems consisting of more than two species, the analyses are quite complicated and the stability depends critically on parameter sets chosen. To avoid this, I use plausible values as parameters for one of the best-known examples, a *Daphnia*-algal system. Although parameter values are basically chosen from Grover (1995) as representatives, the parameter values with regard to the nutrient-dependent growth rate of prey are chosen from several other literatures because the values did not correspond to one identical species in Grover (1995). I chose a green alga, *Scenedesmus quadricauda*, and a diatom, *Cyclotella meneghiniana*, as the representatives of the more profitable prey and blue-green algae, *Anabaena flos-aquae* and *Oscillatoria agardhii*, as the representatives of the less profitable prey, because these are

widespread species in freshwater ecosystems and I am able to refer to each set of the parameter values for each species with regard to the nutrient-dependent growth rate from one original literature.

4.2 MODEL

Model formation

As a model, I use a revised version of the model in Chapter 3, which seems more similar to the Grover (1995) model, to incorporate values of parameters based on laboratory studies of *Daphnia* and algae:

$$dX_1/dt = \mu_1(N)X_1 - \varepsilon_1X_1 - r_1(X_1, X_2)Y \quad (4.1a)$$

$$dX_2/dt = \mu_2(N)X_2 - \varepsilon_2X_2 - r_2(X_1, X_2)Y \quad (4.1b)$$

$$dY/dt = -\varepsilon_3Y + s_1r_1(X_1, X_2)Y + s_2r_2(X_1, X_2)Y \quad (4.1c)$$

$$N + q_1X_1 + q_2X_2 + q_3Y = T \quad (4.1d)$$

The state variables are the densities of the more profitable prey (X_1 [cells l^{-1}]), the less profitable prey (X_2 [cells l^{-1}]) and the predator (Y [animals l^{-1}]), and the concentration of nutrient available for the prey (N [$\mu\text{mol } l^{-1}$]). The degree of enrichment is expressed by the total amount of nutrient in the system (T [$\mu\text{mol } l^{-1}$]). I adopted a saturating function of nutrient for the nutrient-dependent growth rate of prey i (Monod equation):

$$\mu_i(N) = \frac{b_i N}{K_i + N} \quad i = 1, 2.$$

For the functional response of the predator *Daphnia*, I use a type 2 equation including two prey:

$$r_i(X_1, X_2) = \frac{a_i X_i}{1 + h_1 a_1 X_1 + h_2 a_2 X_2} \quad i = 1, 2.$$

Notation of parameters is listed in table 4.1.

Differences between the prey in profitability and in predator filtering rate are, respectively, described by the following inequalities (see Chapter 3):

$$s_1/h_1 > s_2/h_2 \quad \text{and} \quad a_1 > a_2. \quad (4.2)$$

Parameterization

I adopt the estimation by Grover (1995) as values for most of parameters (table 4.1). As for the nutrient-dependent growth rate of prey, I use another parameter set for each prey type (table 4.2).

As previously stated, I assume that the less profitable prey, as well as the more profitable prey, is consumed and can contribute some nutritional benefit to the predator. I represent the degree of this unknown nutritional benefit of the less profitable prey by changing the assimilation rate of the prey, s_2 , which must satisfy inequality (4.2), i.e. $0 \leq s_2 < s_1 h_2 / h_1$. The case $s_2 = 0$ corresponds to the third class of inedible prey

(nutritionally valueless prey) in the Grover (1995) model.

4.3 STABILITY

Stability of the system in equations (4.1) was calculated numerically by testing the Routh-Hurwitz criteria (equations (4.A1) in Appendix 4.A) in the presence of *Daphnia* as the predator, either of *S. quadricauda* or *C. meneghiniana* as the more profitable prey, and either of *A. flos-aquae* or *O. agardhii* as the less profitable prey. Results are expressed in a parameter space of the degree of enrichment (T) and the relative profitability of the less profitable prey to the more profitable prey, $\gamma = (s_2/h_2)/(s_1/h_1)$, in figure 4.1. Total phosphorus concentration is used here as the degree of enrichment, with a plausible range $<3 \mu\text{mol P l}^{-1}$ (Grover 1995).

In the case of *S. quadricauda* vs. *A. flos-aquae* (figure 4.1a), at low degrees of enrichment the less profitable prey ($X_2 = A. flos-aquae$) cannot invade into the system because of its inferiority in nutrient competition. The degree of enrichment below which X_2 cannot invade is generally determined by the difference in competition ability between the prey. The more profitable prey ($X_1 = S. quadricauda$) is excluded when the system is sufficiently enriched and the profitability of the less profitable prey is high. This would be due to a relaxation of nutrient competition between the prey caused by enrichment and the effect of so-called apparent competition (Holt 1977). The boundary above which the more profitable prey (X_1) goes extinct approaches to a line $\gamma = \epsilon_3/(s_1/h_1)$ where the profitability of the less profitable prey is ϵ_3 . Below this critical profitability ϵ_3 , the prey

(X_2) cannot yield sufficient nutrition by itself to support the predator population (see Chapters 2, 3).

There is a region in which all the species coexist (figure 4.1a). Similar to previous models of one predator and one prey (e.g. Rosenzweig 1971), coexisting equilibria tend to be stable at low degrees of enrichment. Numerical simulation showed that systems with parameter sets in the unstable region displayed cyclic dynamics (limit cycles). It is noticeable that, when the profitability of the less profitable prey exists in the vicinity of the critical profitability ε_3 , coexisting equilibrium points remain stable even at considerably high degrees of enrichment. The reason why the unstable region occurs at large T and low γ values would be as follows. When the profitability of the less profitable prey is low, the abundance of the more profitable prey (X_1) increases more sensitively to an increase in the total amount of nutrient than the less profitable prey (Chapter 3). Thus, the stabilizing effect of the less profitable prey by reducing the net attack rate on the more profitable prey diminishes with enrichment.

In the case of *C. meneghiniana* vs. *O. agardhii*, the coexisting equilibria are always unstable (figure 4.1b). The qualitative results of the other two combination of prey are classified into either of the results above (table 4.3). There were also coexisting equilibria at high degrees of enrichment in the case of *C. meneghiniana* vs. *A. flos-aquae* when the profitability of the less profitable prey was close to the critical value ε_3 , although the region of the stable equilibria was smaller than in the case of *S. quadricauda* vs. *A. flos-aquae*.

Finally I conducted numerical simulation to see the dependency of a region in which all three species can coexist stably in *Daphnia*-two-algal systems on the parameters for

the nutrient-dependent growth rate of prey (figure 4.2). Given that one of two prey is *S. quadricauda*, a region of stably coexisting equilibria appears over a wide range of parameter values (figure 4.2a), reflecting compatibility of the species with less profitable prey in table 4.3. Although *O. agardhii* is unable to have stable equilibria with either of the more profitable prey chosen (table 4.3), there exist parameter values to have stable equilibria but the region is considerably smaller (figure 4.2b) than *S. quadricauda* (figure 4.2a). In the both cases, the presence of stably coexisting equilibria is more dependent on the maximum growth rate (b) than the half-saturation constant (K) of prey. In systems with parameter sets in the region of stable equilibria in figure 4.2, there was a common tendency that coexisting equilibrium points were likely to be stable with the profitability of the less profitable prey close to the critical value ε_3 even at high degrees of enrichment, similar to figure 4.1a.

4.4 DISCUSSION

In the Grover (1995) model there were no stable equilibria when the less profitable prey was nutritionally valueless ($s_2 = 0, b_1 = 0.93, K_1 = 0.02, b_2 = 0.9, K_2 = 0.06$ were used). I preliminarily re-examined the stability of the Grover (1995) model with nutritionally valueless prey, but no stable equilibria appeared even when the profitability of the less profitable prey, which had been assumed zero as was called 'valueless', could take positive values. In my model of typical freshwater one-predator-two-prey systems, all species were able to coexist stably in two cases of four possible combinations of prey, whereas there

were no stable equilibria for the rest of two cases which always involved the species *O. agardhii* (table 4.3). It was, however, shown that such a species as *O. agardhii* could have stable equilibria, depending on the nutrient-dependent growth rate of its competitor (figure 4.2b). This indicates that in a *Daphnia*-two-algal system every algal species in nature can coexist stably with a certain algal species. Furthermore, an alga has a potential to coexist stably with any algal species because parameter values for the algal growth rate depend on temperature (Ahlgren 1978, 1985, 1987), light intensity (Schlesinger & Shuter 1981; Ahlgren 1985), and probably conditions of other nutrients such as nitrogen and silicon.

When all three species were able to coexist stably, equilibria were always stable around the critical profitability of the less profitable prey ε_3 even in the face of sufficient enrichment. In Chapter 3, I theoretically suggested that the unknown profitability of less profitable prey could be close to the critical value ε_3 , from the viewpoint of the response of the more profitable prey abundance to enrichment which had been theoretically unclear. I showed in Chapter 3 that whether the more profitable prey increased or decreased with enrichment depended on the profitability of the less profitable prey and the more profitable prey did not change in abundance when the profitability took the critical value (ε_3). According to compiled empirical data by Watson & McCauley (1988) and Watson *et al.* (1992), the more profitable prey biomass scarcely varies with total phosphorus. Thus the theoretical prediction and the compiled empirical data can lead to an estimation of the unknown profitability of less profitable prey to be close to the critical value (ε_3). Together with this estimation, my results here imply that natural *Daphnia*-algal systems can keep stable equilibria with no increase in the more profitable prey biomass against

enrichment, without any specific assumptions such as spatial heterogeneity (e.g. Ruxton 1995; Křivan 1998) and density-dependent autotoxins produced by predator (Kirk 1998). This could be a resolution of discrepancy between theory and observation with regard to the effect of enrichment on stability in predator–prey systems.

Table 4.1 Notation of parameters and their estimated values

Symbol	Meaning	Units	Values used
b_1, b_2	Maximum growth rate of prey	d^{-1}	see table 4.2
K_1, K_2	Half-saturation constant for growth rate of prey	$\mu\text{mol P l}^{-1}$	see table 4.2
$\varepsilon_1, \varepsilon_2$	Density-independent death rate of prey	d^{-1}	0.02, 0.1†
a_1, a_2	Predator filtering rate	$\text{l animal}^{-1} \text{ d}^{-1}$	0.04, 0.032†
h_1, h_2	Handling time for prey	$\text{animal days cell}^{-1}$	2.2×10^{-6} , 2.8×10^{-6} †
ε_3	Per capita death rate of predator	d^{-1}	0.1
s_1, s_2	Assimilation rate of prey	animal cell^{-1}	5.7×10^{-7} , various†
q_1, q_2	Cellular nutrient content of prey	$\mu\text{mol P cell}^{-1}$	9.1×10^{-9} , 1.8×10^{-8} †
q_3	Per capita nutrient content of predator	$\mu\text{mol P animal}^{-1}$	1.6×10^{-2}

†Parameter values for the less profitable prey X_2 .

Table 4.2 Algal prey species for the calculation of stability and their estimated values for the maximum growth rate (b) and half-saturation constant (K)

Species	b (d ⁻¹)	K ($\mu\text{mol P l}^{-1}$)	Reference
More profitable prey (X_1)			
<i>Scenedesmus quadricauda</i>	0.6	0.034	Sommer (1989)
<i>Cyclotella meneghiniana</i>	0.78	0.25	Tilman & Kilham ¹ (1976)
Less Profitable prey (X_2)			
<i>Anabaena flos-aquae</i>	1	0.06	Morel (1987)
<i>Oscillatoria agardhii</i>	0.5	0.032	Ahlgren (1977)

¹Based on data of Gotham & Rhee (1981).

Table 4.3 Summarized results of whether a region of stable equilibria is present (○) or absent (×) in systems of *Daphnia*, one of more profitable prey, and one of less profitable prey

	More profitable prey (X_1)	
	<i>S. quadricauda</i>	<i>C. meneghiniana</i>
Less profitable prey (X_2)		
<i>A. flos-aquae</i>	○	○
<i>O. agardhii</i>	×	×

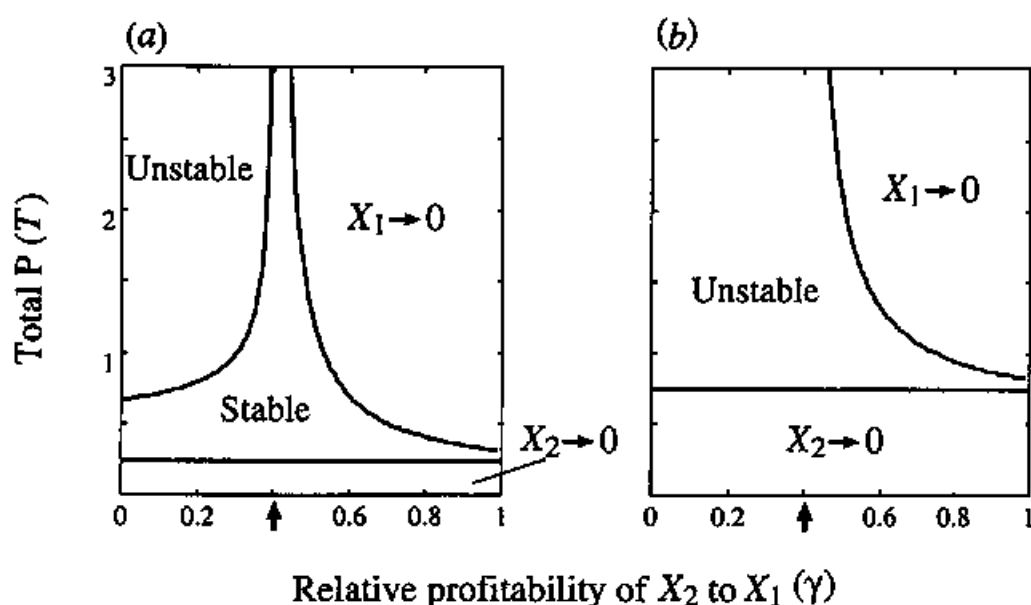


Figure 4.1 Numerical analyses of systems with *Daphnia* and algae. The horizontal axes represent relative profitability of the less profitable prey to the more profitable prey, $\gamma = (s_2/h_2)/(s_1/h_1)$ [dimensionless]. The vertical axes represent total phosphorus, T [$\mu\text{mol P l}^{-1}$]. Arrows express where the profitability of the less profitable prey takes the critical value ($= \varepsilon_3/(s_1/h_1)$). Parameter values used are shown in tables 4.1 and 4.2. The algal prey are (a) *Scenedesmus quadricauda* and *Anabaena flos-aquae*, and (b) *Cyclotella meneghiniana* and *Oscillatoria agardhii*.

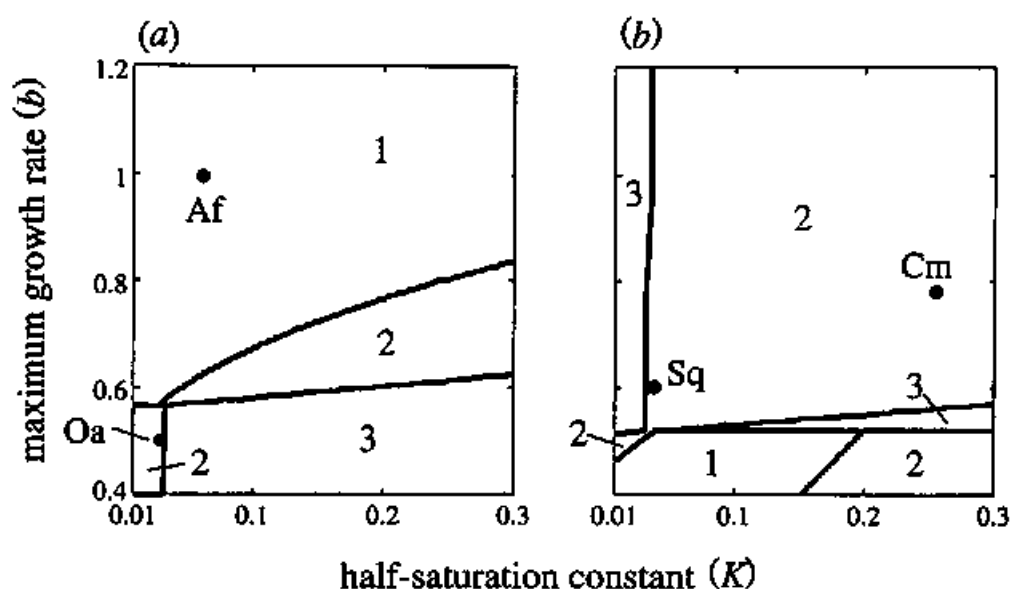


Figure 4.2 Numerical analyses for stability of systems with *Daphnia* and two algae. One of the two algae is given and the other is an imaginary alga with various parameters for the nutrient growth rate, b and K . (a) *S. quadricauda* is given. (b) *O. agardhii* is given. Region 1, there are stably coexisting equilibria; region 2, coexisting equilibria are always unstable; region 3, there is no equilibrium for all three species to coexist. The parameter sets for *S. quadricauda* (Sq), *C. meneghiniana* (Cm), *A. flos-aquae* (Af), and *O. agardhii* (Oa) are also indicated.

APPENDIX 4.A

Stability analysis

Though the system described in equations (4.1) has four variables, X_1 , X_2 , Y and N , it can be reduced to a three-dimensional system (X_1, X_2, Y) because of the mass balance equation (4.1d). Standard analysis for stability in this system leads to three conditions with regard to derivatives at equilibrium, $\alpha_{ij} = \partial \dot{X}_i / \partial X_j \big|_*$ ($i, j = 1, 2, 3$; X_3 corresponds to the predator Y), where ‘*’ denotes a value at equilibrium. The system is stable if and only if

$$A_1 > 0 \quad (4.A1a)$$

$$A_3 > 0 \quad (4.A1b)$$

$$A_1 A_2 > A_3, \quad (4.A1c)$$

where

$$A_1 = -\alpha_{11} - \alpha_{22} - \alpha_{33}$$

$$A_2 = \alpha_{11}\alpha_{22} + \alpha_{22}\alpha_{33} + \alpha_{33}\alpha_{11} - \alpha_{12}\alpha_{21} - \alpha_{23}\alpha_{32} - \alpha_{31}\alpha_{13}$$

$$A_3 = -\alpha_{11}\alpha_{22}\alpha_{33} - \alpha_{12}\alpha_{23}\alpha_{31} - \alpha_{32}\alpha_{21}\alpha_{13} + \alpha_{11}\alpha_{23}\alpha_{32} + \alpha_{22}\alpha_{31}\alpha_{13} + \alpha_{33}\alpha_{12}\alpha_{21}.$$

The full expressions of the derivatives, $\alpha_{ij} = \partial \dot{X}_i / \partial X_j$, are

$$\alpha_{11} = X_1^* (-q_1 d\mu_1/dN|_* + h_1 a_1^2 Y^*/D^2)$$

$$\alpha_{12} = X_1^*(-q_2 d\mu_1/dN|_* + h_2 a_1 a_2 Y^*/D^2)$$

$$\alpha_{13} = X_1^*(-q_3 d\mu_1/dN|_* - a_1/D)$$

$$\alpha_{21} = X_2^*(-q_1 d\mu_2/dN|_* + h_1 a_1 a_2 Y^*/D^2)$$

$$\alpha_{22} = X_2^*(-q_2 d\mu_2/dN|_* + h_2 a_2^2 Y^*/D^2)$$

$$\alpha_{23} = X_2^*(-q_3 d\mu_2/dN|_* - a_2/D)$$

$$\alpha_{31} = Y^*\{s_1 a_1/D - h_1 a_1(s_1 a_1 X_1^* + s_2 a_2 X_2^*)/D^2\}$$

$$\alpha_{32} = Y^*\{s_2 a_2/D - h_2 a_2(s_1 a_1 X_1^* + s_2 a_2 X_2^*)/D^2\}$$

$$\alpha_{33} = 0,$$

where $D = 1 + h_1 a_1 X_1^* + h_2 a_2 X_2^*$.

Chapter 5

Summary and conclusion

Using one-predator-two-prey systems with different prey profitability, I theoretically examined the effects of enrichment on stability and population abundances at equilibrium. In any feeding type of predator, the effects were shown to depend critically on the profitability of the less profitable prey which had been unknown in natural systems and not been clearly dealt with by previous models.

In Chapter 2, I analysed the stability of a system involving an optimally selective feeding predator as a possible resolution of the paradox of enrichment. A theoretical model of a predator-prey system with a natural assumption of satiation in predation predicted that enrichment caused the populations to fluctuate to stochastic extinction. However, this paradox of enrichment did not always occur in experimental and natural communities. I presented a theoretical model that described a novel mechanism for resolving the paradox in the case of a predator with optimal selective feeding. Specifically, a less profitable but edible (thus, 'unpalatable') prey species sharply reduced the amplitude of population oscillations and firmly prevented the minimum abundances of species from falling below certain values. The presence of such an unpalatable prey thus guaranteed the robustness of the system against enrichment.

In Chapter 3, using a system involving a generalist predator I clarified the response of the more profitable prey abundance at equilibrium to enrichment which had been various among previous models. Theoretical and empirical evidence in a one-predator-two-prey

system consistently indicated a regular trend that the less profitable (therefore, less vulnerable) prey increases in abundance with enrichment. The response in the abundance of the more profitable (more vulnerable) prey to enrichment had, however, remained unclear. Previous theoretical models had assumed the less profitable prey as inedible, though its actual profitability was unknown. Relaxing this assumption, I showed that the response of the more profitable prey abundance to enrichment depended critically on the profitability of the less profitable prey. Specifically, the more profitable prey increased in abundance with enrichment if the profitability of the less profitable prey was lower than a critical value so that it was unable to support the predator population by itself even at high densities (in this case, the prey was referred to as 'unpalatable'), and decreased otherwise. This established a more general rule, which unified the previous works and resolved the indeterminacy, on the response of the more profitable prey.

In Chapter 4, I analysed the stability of the system considered in Chapter 3. There is evidence in freshwater one-predator-two-prey systems that there is no change in the abundance of more profitable prey. Regarding stability of predator-prey systems, although enrichment often led in theory to destabilization of systems, this destabilization did not always occur empirically. I conducted numerical analyses of stability along a gradient of enrichment using *Daphnia*-algal systems with realistic parameter values. It was shown to depend on combination of algal prey species whether or not all species were able to coexist stably. In systems with proper combination of prey species, if the profitability of less profitable prey was close to a critical value, it was further shown that the *Daphnia*-algal systems can hold a stable equilibrium even at high degrees of enrichment with no change in the abundance of more profitable prey. This accounted simultaneously

for the response of population abundance and stability to enrichment in natural systems.

I showed that the presence of less profitable prey with a profitability close to a critical value sharply increased the stability in the case of a predator with optimally selective feeding in Chapter 2. In Chapter 4, I showed a possibility that equilibria in nature keep stable even with an increase of total phosphorus in lakes in the case of a generalist predator. These indicate a potential that predator-prey systems are robust with regard to stability against a recently serious trend of enrichment, irrespective of the type of predator.

Most real communities are more complex than the communities analysed here. McCann *et al.* (1998) showed with communities of up to four species that interactions of weak to intermediate strength between species were important in promoting community persistence and stability. The presence of less profitable prey in my models can be regarded as a cause of such a link, because the prey is not a main food for predators. Although it will be difficult to analyse communities incorporating many (i.e. more than three) species and more realistic links such as intraguild predation, it is an important and open problem to be solved step by step.

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‘We have not inherited the earth from our ancestors.

We are borrowing it from our unborn children.’

— Native American Saying